Big is not better: small *Acacia mellifera* shrubs are more vital after fire

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Abstract

Fire and acacias are vital components in savanna dynamics but little is known about the relationship between postfire mortality and size of *Acacia* species. We determined mortality, height, and height of resprouts of the encroaching shrub species *Acacia mellifera* in a semi-arid South African savanna 2 years after fire. As expected, resprouting ability after topkill was high, only 9% of the studied shrubs died completely. Surprisingly, shrubs that died in the fire were significantly taller than their resprouting conspecifics. Results from quantile regression show that the height of regrowth relative to the total height of taller shrubs is less than in smaller shrubs, despite taller shrubs having more access to below-ground resources. We offer two possible explanations for these unexpected results: in taller shrubs, the maximum longitudinal growth rate of resprouts may be reached and therefore, resources may be invested in a greater number of resprouts or stored as reserves. Alternatively, resprouting ability may be impaired in old age by a senescence effect caused by the accumulation of physiological dysfunctions.

Key words: below-ground traits, flame zone, Kalahari thornveld, limiting factors, roots, size

Résumé

Le feu et les robiniers sont des composants importants de la dynamique de la savane, mais il y a peu d'informations sur le rapport entre la mortalité après feu et la taille de l'espèce *Acacia*. Nous avons établi la mortalité, la grandeur, et la grandeur des repousses de l'espèce de buisson empiétant l' *Acacia mellifera* dans une savane semi-aride en Afrique méridionale deux ans après un incendie. Comme prévu, la capacité de repousser après topkill s'avérait élevée; seulement 9% des buissons étudiés furent complètement morts. Etonnamment, les buissons qui sont morts dans l'incendie furent beaucoup plus grand que leurs conspécifiques repoussants. Les résultats de la régression quantile démontrent que la grandeur des repousses relativement à la grandeur totale des buissons plus grands, est moins que chez les plus petits buissons, bien que les buissons plus grands ont plus d'accès aux ressources souterraines. On propose deux explications éventuelles pour ces résultats inattendus: chez les buissons plus grands, il est possible que le taux de croissance longitudinal maximum soit atteint et ainsi les ressources sont investies dans un plus grand nombre de repousses où alors rangés en réserve. Autrement, la capacité de repousser peut être affaiblie dans l'âge avancé par un effet de la sénescence du à une accumulation de dysfonctionnements physiologiques.

Introduction

Although fire and acacias are vital components in African savanna dynamics, little is known about the impact of fire on *Acacia* life cycles (Midgeley & Bond, 2001). Midgeley & Bond (2001) express the need for more research relating fire-sensitivity to size and age of *Acacia* species. In savanna woody species, topkill is much more frequent than complete mortality after fire (Hoffmann & Solbrig, 2003). Rather, fire stimulates resprouting from below-ground tissues (Pendergrass, Miller & Kauffman, 1998). Studies on the relationship between shrub size and resprouting ability have not generated consistent results: the relationship is negative for woody species in wet prairies (Pendergrass *et al.*, 1998), not significantly different from zero for a fynbos conifer (Keeley, Keeley & Bond, 1999), and positive for several shrubs including *Acacia* species (Hodgkinson, 1998), a *Prosopis* species (Wright, Bunting & Neuenschwander, 1976), a mediterranean tree (Pausas, 1997),

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and a *Pinus* species (Thanos, Daskalakou & Nikolaidou, 1996). In temperate woodlands in Australia, resprouting ability is highest in medium size classes (Hodgkinson, 1998). In general, tall trees are only severely damaged by fires of higher intensity (Morrison & Renwick, 2000), as most parts of their canopy are above the flame zone of small to medium intensity fires.

Little is known about the relationship between total shrub height and height of regrowth after fire. Assuming a positive correlation between above- and below-ground size, taller plants should have more reserves that they can allocate to regrowth after fire, e.g. in *Eucalyptus*, the growth rate of resprouts increases with prefire height (Hodgkinson, 1992). Below-ground reserves are especially important for resprouting ability after fire (McGee, Leopold & Nyland, 1995). We expect that the height of regrowth should be proportional to the height of the shrub with a factor of at least 1.00.

Acacia mellifera Benth. is a resprouting multi-stemmed shrub with an average height of 75 cm (K.M. Meyer *et al.*, unpublished data) and frequently encroaches into open savannas, i.e. densities of these plants can locally be so high as to convert an open (grass-dominated) savanna into a closed savanna or woodland (Smit, 2004). Skarpe (1991) attributes the great fire susceptibility of *A. mellifera* to its small size, which constrains at least parts of its canopy permanently to the flame zone of grass fires. However, this relationship has not been studied in detail for *A. mellifera*. The present study investigates postfire mortality and resprouting as a function of *A. mellifera* size and below-ground morphometrical traits.

Material and methods

Study area

The study was conducted in semi-arid savanna in the Kalahari thornveld at Pniel Estates (S 28°35′, E 24°29′), 30 km north of Kimberley, South Africa, in January 2004. Mean annual precipitation is 388 mm and occurs as thunderstorms throughout the summer months (September to March). Blackthorn (*A. mellifera*), camphor tree (*Tarchonanthus camphoratus*), and umbrella thorn (*A. tortilis*) were the dominant plant species on the shallow sandy soils of the study area. In November 2002, a fire of an estimated medium to high intensity affected the study area for 10–12 h until it was extinguished by the farm management.

Field methods

All *A. mellifera* shrubs were recorded along a 1500 m long and 20 m wide transect and were classified as dead and alive to determine postfire mortality. A shrub was counted as dead if no regrowth could be identified and as alive if resprouts were present. We assumed that, with a time-lag of more than 1 year after a fire, a living shrub that lost all photosynthetic structures to the fire should have produced regrowth to survive. Therefore, we did not look for other live tissue than the clearly visible regrowth at the stem bases. The maximum height of the residual branches of all dead shrubs was determined to investigate the relationship between size and mortality. The maximum height of 30 randomly-chosen live *A. mellifera* shrubs and the height of their regrowth were determined. We assumed that the probability of an underestimation of maximum shrub height because of burnt-off branches was constant for all shrubs in the study area. In an adjacent part of the study area that was not affected by the fire, an index of below-ground growth was determined by measuring the length of subsurface roots within a randomly-chosen 60°-angle centered at the tap root from sixteen *A. mellifera* shrubs. The entire lengths of these roots were excavated until they turned vertically downwards (to a depth of >1 m). The height of the shrubs and the length of the longest root (between tap root and the point of turning vertically downwards) were determined to explore the relationship between above- and below-ground morphometrical traits.

Data analyses

The heights of dead and live *A. mellifera* shrubs were compared with Wilcoxon's signed rank test. The relationships between height of regrowth and total height of *A. mellifera* and between height and length of longest root were explored in quantile regressions because the data points assumed a triangular shape, suggesting an upper limiting factor and the impact of other unmeasured factors (cf. Goldberg & Scheiner, 1993). Conventional linear regression assumes homogeneity of variance across the range of x-values (Sokal & Rohlf, 1998). As this assumption was violated we used quantile regression (Goldberg & Scheiner, 1993; Thomson *et al.*, 1996). In quantile regression, different parts of the variation in the data are captured by different quantiles (Koenker & Bassett, 1978). Quantile regression functions are estimated by minimizing an asymmetrically-weighted sum of absolute residual errors (Koenker & Bassett, 1978; Cade, Terrell & Schroeder, 1999; Cade, 2003). The τth quantile regression function, $Q(\tau)$, describes a linear or nonlinear fit through the data so that τ proportion of the data is less than $Q(\tau)$ and 1-τ proportion is greater than $Q(\tau)$. The upper quantile is a more appropriate representation of the limiting factor than the central estimate of a conventional regression (Cade *et al.*, 1999). The more that upper quantiles have the same slope, the smaller the proportion of the sample that is affected by the interaction with unmeasured factors (Cade, 2003). The more that quantiles have the same slope, the more the impact of the unmeasured factors tends to be additive rather than interactive (Cade, 2003). The software package S-PLUS 6.1 was used for statistical analyses.

Results

The mortality of *A. mellifera* was 0.09 in the study area (n = 747 shrubs), i.e. 91% of the shrubs showed regrowth 14 months after a fire. Dead *A. mellifera* shrubs were significantly taller than live *A. mellifera* ($p < 0.0001$, Fig. 1). Taller live shrubs had taller regrowth (0.9-quantile in Fig. 2a). This trend can be generalized for all but the 0.5- and the 0.7-quantiles, where the slope of the regression was not significantly greater than 0 (see lower confidence interval in Fig. 2b). However, the slope of this relationship was only 0.25 (0.9-quantile in Fig. 2a) and significantly less than 1.00 for all quantiles (see upper confidence interval in Fig. 2b) so that taller trees had less relative regrowth per unit height than smaller trees. Unmeasured factors had a strong impact on the total height – regrowth height relationship because the upper quantiles did not have the same slope (Fig. 2a). The effect of the unmeasured factors was interactive rather than additive because the slopes of the quantiles differed greatly (Fig. 2a).

The relationship between the length of the longest root and the height of a shrub was significantly greater than 0 only for quantiles smaller than or equal to 0.5 (Fig. 3). The lower confidence interval of the quantile slopes was significantly larger than 1 only for the 0.1-, 0.3-, and 0.4-quantile (Fig. 3b). The minimum root length was determined by the height of a shrub but the upper limit was constrained by unmeasured factors.

Discussion

Fire did not have a strong impact on *A. mellifera* performance in the study area because mortality after fire is

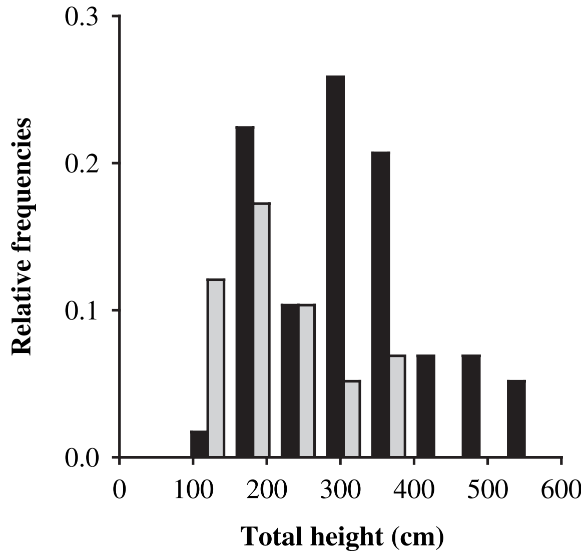

Fig 1 Relative frequencies of total height of *A. mellifera* shrubs without regrowth (black bars, n = 58) and with regrowth after fire (grey bars, n = 30)

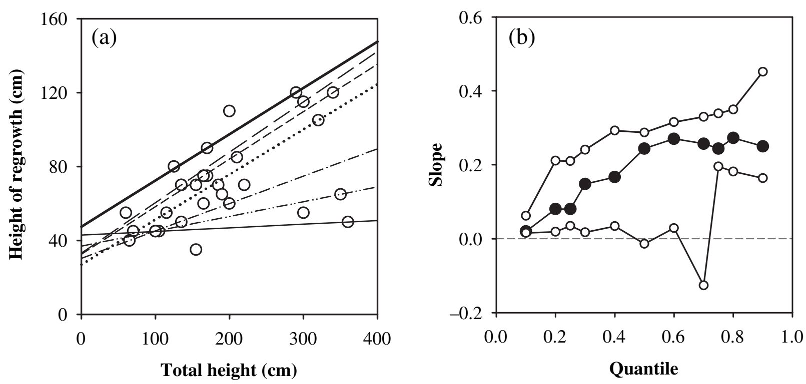

Fig 2 Relationship between the height of regrowth and the total height of *A. mellifera* shrubs (n = 30). (a) Quantile regression estimates. Quantiles from top to bottom: solid bold line: 0.9-quantile, long-dashed: 0.8-quantile, short-dashed: 0.7-quantile, dotted: 0.5-quantile, dot-dashed: 0.3-quantile, dot-dot-dashed: 0.2-quantile, solid: 0.1-quantile. (b) Slope of the quantile regression lines in (a) (solid circles) with upper and lower 90% confidence intervals (open circles)

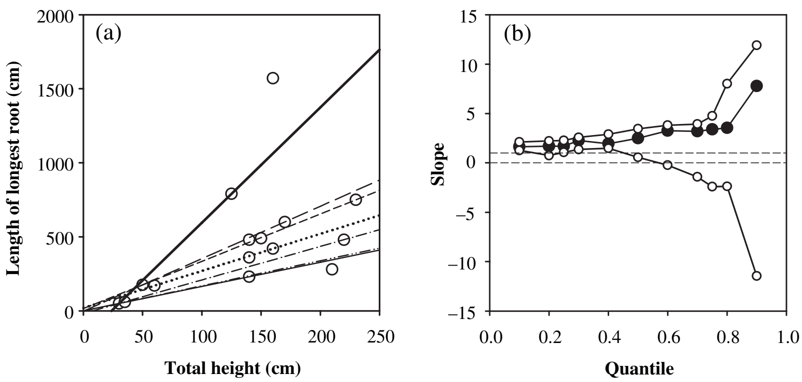

Fig 3 Relationship between the length of the longest root and the total height of *A. mellifera* shrubs (n = 16). The length of the longest root refers to the maximum length of a surface root between the tap root and the point of turning vertically downwards within a randomly chosen horizontal 60°-angle centered at the tap root. (a) Quantile regression estimates. Quantiles from top to bottom: solid bold line: 0.9-quantile, long-dashed: 0.8-quantile, short-dashed: 0.7-quantile, dotted: 0.5-quantile, dot-dashed: 0.3-quantile, dot-dot-dashed: 0.2-quantile, solid: 0.1-quantile. (b) Slope of the quantile regression lines in (a) (solid circles) with upper and lower 90% confidence intervals (open circles). The slopes of 0 and 1 (dashed lines) are given as reference lines

low (9%). Such low mortalities and high resprouting abilities of savanna woody species are in accordance with earlier findings (Keeley *et al.*, 1999; Owens, Mackley & Carroll, 2002). The shrubs that were killed completely were significantly taller than their resprouting conspecifics. This is surprising because most studies on size-dependent mortality of savanna woody species reported decreasing postfire mortalities with increasing size (Hodgkinson, 1998; Hoffmann & Solbrig, 2003). Adams (1967) has shown that height and shape are reliable indicators of age in *A. mellifera*; consequently, we can conclude that younger *A. mellifera* shrubs have a higher probability of resprouting after fire, which contradicts the general trend in woody species (Turner, Romme & Gardner, 1999; Seligman & Henkin, 2000) but has also been shown for *Adenostoma* shrubs in the chaparral (Odion & Davis, 2000).

We can safely assume that taller shrubs have access to disproportionately more below-ground resources than small shrubs because of the positive relationship between minimum root length and shrub height (Fig. 3) and because there is evidence for a positive correlation between stem diameter and below-ground biomass in *Acacia* species (Coughenour, Ellis & Popp, 1990). In spite of this, smaller *A. mellifera* shrubs have taller relative regrowth per unit height than taller shrubs after fire.

Light, water, and nutrient availability cannot differ greatly between trees of different sizes because all trees grow in the same area. Only small-scale heterogeneities that are correlated with tree size could explain the paradox of less regrowth in taller shrubs in spite of their having more below-ground resources than small shrubs. In general, the importance of environmental factors for shrub regrowth after fire can be doubted: in *Eucalyptus*, the growth rate of resprouting shrubs is primarily determined by physiological and morphological factors associated with plant size and only assisted by greater water and nutrient availability after fire (Hodgkinson, 1992).

Another more simple explanation for less regrowth in tall shrubs in spite of more below-ground resources could be that the rate at which new cells can be produced in the apical meristems is physically limited (Lyndon, 1976). The proportion of rapidly cycling meristematic cells is strongly correlated with growth (Francis, 1998). Thereby, the longitudinal growth rate of a shrub is constrained to a maximum value. This maximum growth rate may have been reached by the regrowth of the taller shrubs in the study area so that the regrowth does not attain the height expected from the total size of the shrubs. Once the maximum longitudinal growth rate is reached, taller shrubs may keep their greater below-ground resources as a reserve or invest them in a greater number of resprouts. In fact, Morrison & Renwick (2000) and Stocker (1999) found that the number of resprouts increased with the size of the stem of several woody species, including *Acacia* shrubs.

Finally, senescence may impair the regrowth of older shrubs. Older shrubs of the Californian chaparral allocate less photosynthate to storage compounds in spring than younger shrubs, indicating a physiological senescence effect (Sparks, Oechel & Mauffette, 1993). Senescence effects emerged especially in stands where fire was absent over long periods (Sparks *et al.*, 1993), suggesting fire and senescence as rejuvenation agents for plant communities: in other words, an old plant either dies from old age or from fire, thereby making space available for younger plants. If a plants is young enough to survive the fire, it is increasingly affected by physiological disfunctions that accumulate with age and weaken its resprouting ability. This may explain the relatively lower regrowth in taller (and presumably older) shrubs in the present study.

Our results from the quantile regression also show that unmeasured factors play an important interactive role in the total height – regrowth height relationship. Below-ground biomass, stem diameter, number of resprouts, patchily-distributed resources, and water availability may be among these factors, and should be explored in further research.

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References

Adams, M.E. (1967) A study of the ecology of *Acacia mellifera, A. seyal* and *Balanites aegyptiaca* in relation to land-clearing. *J. Appl. Ecol.* **4,** 221–273.

Cade, B.S. (2003) *Quantile regression models of animal habitat relationships*, PhD Dissertation. Colorado State University, Fort Collins, CO.

Cade, B.S., Terrell, J.W. & Schroeder, R.L. (1999) Estimating effects of limiting factors with regression quantiles. *Ecology* **80,** 311–323.

Coughenour, M.B., Ellis, J.E. & Popp, R.G. (1990) Morphometric relationships and developmental patterns of *Acacia tortilis* and *Acacia reficiens* in Southern Turkana, Kenya. *B. Torrey Bot. Club* **117,** 8–17.

Francis, D. (1998) The cell cycle and plant growth. In: *Inherent Variation in Plant Growth. Physiological Mechanisms and Ecological Consequences* (eds. H. Lambers, H. Poorter & M. M. I. Van-Vuuren). Backhuys Publishers, Leiden.

Goldberg, D.E. & Scheiner, S.M. (1993) anova and ancova: Field competition experiments. In: *Design and Analysis of Ecological Experiments* (eds. S.M. Scheiner & J. Gurevitch). Chapman and Hall, London.

Hodgkinson, K.C. (1992) Water relations and growth of shrubs before and after fire in a semiarid woodland. *Oecologia* **90,** 467–473.

Hodgkinson, K.C. (1998) Sprouting success of shrubs after fire: height dependent relationships for different strategies. *Oecologia* **115,** 64–72.

Hoffmann, W.A. & Solbrig, O.T. (2003) The role of topkill in the differential response of savanna woody species to fire. *Forest Ecol. Manag.* **180,** 273–286.

Keeley, J.E., Keeley, M.B. & Bond, W.J. (1999) Stem demography and post-fire recruitment of a resprouting serotinous conifer. *J. Veg. Sci.* **10,** 69–76.

Koenker, R. & Bassett, G. (1978) Regression quantiles. *Econometrica* **46,** 33–50.

Lyndon, R.F. (1976) The shoot apex. In: *Cell Division in Higher Plants* (Ed. M. M. Yeoman). Academic Press, London.

McGee, G.G., Leopold, D.J. & Nyland, R.D. (1995) Understory response to springtime prescribed fire in 2 New-York transition oak forests. *Forest Ecol. Manag.* **76,** 149–168.

Midgeley, J.J. & Bond, W.J. (2001) A synthesis of the demography of African acacias. *J. Trop. Ecol.* **17,** 871–886.

Morrison, D.A. & Renwick, J.A. (2000) Effects of variation in fire intensity on regeneration of co-occurring species of small trees in the Sydney region. *Aust. J. Bot.* **48,** 71–79.

Odion, D.C. & Davis, F.W. (2000) Fire, soil heating, and the formation of vegetation patterns in chaparral. *Ecol. Monogr.* **70,** 149–169.

Owens, M.K., Mackley, J.W. & Carroll, C.J. (2002) Vegetation dynamics following seasonal fires in mixed mesquite/acacia savannas. *J. Range Manage.* **55,** 509–516.

Pausas, J.G. (1997) Resprouting of *Quercus suber* in NE Spain after fire. *J. Veg. Sci.* **8,** 703–706.

Pendergrass, K.L., Miller, P.M. & Kauffman, J. B. (1998) Prescribed fire and the response of woody species in Willamette Valley wetland prairies. *Restor. Ecol.* **6,** 303–311.

Seligman, N.G. & Henkin, Z. (2000) Regeneration of a dominant Mediterranean dwarf-shrub after fire. *J. Veg. Sci.* **11,** 893–902.

Skarpe, C. (1991) Spatial patterns and dynamics of woody vegetation in an arid savanna. *J. Veg. Sci.* **2,** 565–572.

Smit, G.N. (2004) An approach to tree thinning to structure southern African savannas for long-term restoration from bush encroachment. *J. Environ. Manage.* **71,** 179–191.

Sokal, R.R. & Rohlf, F.J. (1998) *Biometry*. W.H. Freeman, New York.

Sparks, S.R., Oechel, W.C. & Mauffette, Y. (1993) Photosynthate allocation patterns along a fire-induced age sequence in 2 shrub species from the California chaparral. *Int. J. Wildland Fire* **3,** 21–30.

Stocker, R.K. (1999) Mechanical harvesting of *Melaleuca quinquenervia* in Lake Okeechobee, Florida. *Ecol. Eng.* **12,** 373–386.

Thanos, C.A., Daskalakou, E. N. & Nikolaidou, S. (1996) Early post-fire regeneration of a *Pinus halepensis* forest on Mount Parnis, Greece. *J. Veg. Sci.* **7**, 273–280.

Thomson, J.D., Weiblen, G., Thomson, B.A., Alfaro, S. & Legendre, P. (1996) Untangling multiple factors in spatial distributions: Lilies, gophers, and rocks. *Ecology* **77**, 1698–1715.

Turner, M.G., Romme, W.H. & Gardner, R.H. (1999) Prefire heterogeneity, fire severity, and early postfire plant reestablishment in subalpine forests of Yellowstone National Park, Wyoming. *Int. J. Wildland Fire* **9**, 21–36.

Wright, H.A., Bunting, S.C. & Neuenschwander, L.F. (1976) Effect of fire on honey mesquite. *J. Range Manage.* **29**, 467–471.

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